Lucia Mountains an additional one hundred miles southward. Yet *Corylus* has not been reported from these mountains. In the Pleistocene floras[1] of Southern California on Santa Cruz Island and at Carpinteria, Chaney and Mason did not report it. In the Tomales flora of Central California it was very abundant. It is of interest to place on record the finding of a fossil nut of *Corylus* by J. F. Katenkamp in a gravel pit in the hills overlooking Montecito in Santa Barbara County. The position of the nut in these gravels as well as the position of the gravels in the geological sequence is in some doubt. An excerpt from a letter by Mr. David B. Rogers of the Santa Barbara Museum of Natural History indicates the status of our information as to the origin of the specimen. "The pit from which it came is at least one thousand feet above sea level, standing at least 70 degrees to the horizontal. It is a reformed deposit of older material quite compact, and giving the appearance of considerable age. However, it *may* be no earlier than early Pleistocene. It is fairly uniform in texture throughout a considerable depth, only the upper few feet differing, this stratum being considerably less in density, and is unconformable with the more compact strata beneath. The fruit might easily have originated in this upper, more recent formation, and have trickled down into the older material in the course of quarry operations."

The nut is flattened on four faces due to pressure and its tissues are carbonized. Due to the absence of any other parts of the plant and to the uncertainties of its age no specific name is assigned to it. The material is deposited in the Santa Barbara Museum of Natural History as *"Pal. Bot. 1 '33."*

University of California

STUDIES IN WESTERN VIOLETS—I

Milo S. Baker

Sections Chamaemelanium and Nomimium

All of the western forms of *Viola,* except two, fall without dispute, into two groups known as sections *Chamaemelanium* and *Nomimium.* Although this paper deals only with section *Chamaemelanium,* it is impossible to use the key effectively until one can distinguish the two sections one from the other. In the first place each of our western violets can be assigned easily to its proper section by knowing either the coloring of the corolla or the nature of its habitat. For example, all of the yellow flowered species belong to section *Chamaemelanium.* This section also includes all forms with any yellow color whatever in the corolla. For instance, *Viola Beckwithii* T. & G., *V. trinervata* Howell, *V. Flettii* Piper do not appear to be yellow at all, but a close inspection will disclose that the bases of the petals as well as the spur are yellow or yellowish. Then we have three *Cha-*

[1] Chaney, Mason, Potbury. Carnegie Inst. of Wash. Pub. No. 415. 1934.

maemelanium violets that are nearly white, namely, *V. ocellata* T. & G., *V. rugulosa* Greene and *V. canadensis* L., but again the spur and the bases of the petals are distinctly yellow. Although the color character in many groups of plants is often a poor diagnostic character, in *Viola* this yellow corolla color is invariably associated in the western species, with a flower structure which is nearly identical in all of the *Chamaemelanium* species. This will be explained more fully presently.

Considering next their habitats, all but two of the *Chamaemelanium* species are dry-land plants, that is, they are adapted to the rainless summers of the western states and thrive during the season of rainfall and until the moisture dries beyond the reach of their roots, when they die down to their perennial rootstocks and begin their summer sleep, finally to awaken with a new season of moisture and warmth. Indeed several of our species do not wait for a marked increase in temperature, but begin growing soon after the first fall rains. This is true of two of our finest wild pansies, *V. Douglasii* Steud. and *V. pedunculata* T. & G., whose leaves may be found coming through the ground in December and even in the latter part of November in years of early rains.

The only two *Chamaemelanium* violets that prefer places moist throughout the year are *V. glabella* Nutt. and *V. biflora* L. both of which are found in well drained moist situations. Attention should be called to the fact that most authorities assign the latter species not to section *Chamaemelanium* but to section *Dischidium*. However, in the proper place in a subsequent paper, I shall contend that this species should be assigned to section *Chamaemelanium*.

We come now to a consideration of the flower structure of a *Chamaemelanium* violet. In plate II, figure 1, is shown a median vertical section of the flower of *V. Nuttallii* Pursh subsp. *praemorsa* (Dougl.) Piper. The lower petal and its spur as well as the ovary and two of the stamens are shown. The end of the style and stigma may be seen pressed closely against the floor of the lower petal. Indeed the head of the style and the lower lip of the minute stigmatic tube fit so exactly into the groove of the lower petal that such a small insect as thrips is unable to force an entrance underneath or on either side and must perforce crawl over the head to continue on its way to the nectary of the spur (pl. II, fig. 1). The bearding of the head (pl. II, fig. 4) appears to assist in blocking direct passage to the nectary.

The anthers in *Viola* have a peculiar structure (pl. II, fig. 2). The filament is extremely short, and the anther connective is developed anteriorly into a membranous appendage (pl. II, fig. 2, *a*). Further, the five anthers which surround the pistil are closely fitted together with the pollen sacs opening inward. The anterior appendages overlap at each joint and becoming lightly joined together make a pollen-tight sheath, through the distal

end of which projects the head of the style (pl. II, fig. 3). In section *Chamaemelanium* this stamen-sheath fits tightly about the style at every point except for a minute pore formed by the turning back of the flaps of the anterior appendages of the ventral stamens at their point of junction, thus forming the *collar opening* (pl. II, fig. 3, *h*). This opening allows the pollen, as it is discharged from the pollen sacs into the interior of the stamen-sheath, to sift downward into the *pollen trough* of the lower petal at a point immediately behind the head of the style.

The utility of this flower structure in advancing pollination is easily shown. On many occasions I have watched a thrips crawl along the groove of the lower petal till stopped by the close fitting head of the style. This insect then examines the blocking obstacle with its antennae seeking a passage around it. In this prospecting, the stigma is almost certain to be pollinated by some of the grains to be seen adhering abundantly to the surfaces of the antennae. At length this minute insect crawls over the head of the style and drops down into the pollen trough beneath the collar opening and thus gets covered with new pollen.

This brings us to a consideration of the nectary shown at *b* (pl. II, fig. 2). This consists of two outgrowths from the connectives of the two ventral anthers. These outgrowths or *posterior appendages* of the ventral stamens extend downward and backwards into the spur cavity and secrete minute drops of nectar. These hang downward side by side, in contact in some species and in others separated by a small space. These nectaries are shown again in plate II, figure 3 at *l*.

Turning now to section *Nomimium* of the violets, it is to be noted that the western species in this group may also be identified by the color of the corolla and by the nature of the habitat. The corollas may be either white, blue, or purple. All white violets (without *any* yellow) growing in the west, except *Viola Rafinesquii* Greene belong to the section *Nomimium*. All blue violets likewise and all wholly purple flowered species are members of the *Nomimium* group.

While the *Chamaemelanium* violets are mainly dry-land plants, the *Nomimium* violets are mainly moist-land plants, there being but one western *Nomimium* violet that is found growing in spots that become dry when the rainy season has passed. This is *Viola Howellii* Gray which is mainly confined to a humid strip along the coast of Oregon and Washington.

The *Nomimium* flower structure is different in several particulars from that typical of *Chamaemelanium* violets. Here the stigma is held somewhat above the floor of the lower petal (pl. II, fig. 7) and is thus adapted to pollination by larger insects such as flies and bees. The spur is longer and the style head and stigmatic tube are of a different shape and the style bearding, when present, is shorter and differently distributed. Also the

bearding of the lateral petals is much longer and the hairs less clavate. There is no collar opening in the stamen-sheath, the pollen sifting between the loosely overlapping edges of the anterior appendages. Another difference is the longer nectaries correlated of course with the longer spurs. Thus the flower structure of our western violets offers an unfailing guide by which these two sections of *Viola* may be distinguished.

The presence in Colorado of a single violet species belonging to section *Melanium* of *Viola* deserves some attention. In Europe representatives of this section are very numerous, but *Viola Rafinesquii* Greene is the only *Melanium* violet that is native to North America. Nevertheless this section is more widely known than section *Chamaemelanium* or possibly even than section *Nomimium* because of the introduction to America of the *Melanium* pansies of Europe. In flower structure the *Melanium* violets are more closely related to section *Chamaemelanium* than to section *Nomimium*. This close relationship is indicated by naming them dwarf *Melanium* violets (Chamae, signifying dwarf). As in section *Chamaemelanium* the style head fits closely into the groove of the lower petal, and the stamen-sheath possesses a collar opening although less clearly defined. But the style head is more massive, and has no beards, nor the delicate stigmatic tube. Instead the stigmatic surface is an internal cavity of the style head, opening to the outside by a large stigmatic orifice. However, the most conspicuous character of the *Melanium* violets is the large foliaceous stipules. These are sometimes as long and even as large as the leaf itself.

In Part II we hope to consider the group *Nuttallianae* Becker.

Key to the Species of Section Chamaemelanium

Access to the spur cavity blocked by the much expanded, retrorsely bearded, gibbous head of style, which fits closely into groove of lower petal; stamen-sheath open at collar; stigma a mere lip or barely tubular; corolla yellow throughout, or yellow and purple, or purple and lilac, but always with a touch of yellow at least on the spur; bearding of lateral petals short and clavate; spur about as broad as long.

1. Leaves dissected, apparently subcaulescent because of the deep seated rootstock.
   2. Plants of open grassy places; rootstock short and vertical; leaves twice to thrice pinnatifid; flowers yellow or of two contrasting colors, pansy-like.
      3. Aerial stems quite evident; foliage not succulent; at least lower petal yellow.
         4. Minutely pubescent; flowers bright yellow ..... 10. *V. Douglasii*
         4. Glabrous; upper petals dark livid purple, lower cream ..... 11. *V. Hallii*
      3. Aerial stems less evident; foliage somewhat succulent; upper petals madder-violet, lower lilac.
         4. Minutely pubescent; leaf segments not becoming coriaceous ..... 12. *V. Beckwithii*

4. Glandular; leaf segments 3-ribbed and becoming coriaceous ..... 13. *V. trinervata*

2. Plants of wooded or brushy slopes; rootstock elongate, ascending; leaves twice palmatifid; flowers yellow, not pansy-like ..... 7. *V. Sheltonii*

1. Leaves undivided (sometimes lobed in *V. lobata.*)

2. Corolla yellow on face except for dark veining.

3. Plants strictly erect with leaves and flowers crowded at ends of stems, these naked below; basal leaves large, thin, cordate, acute; capsule glabrous, acute.

4. Pubescent to puberulent; upper petals backed with brown; stipules somewhat foliaceous, toothed; leaves entire or lobed ..... 8. *V. lobata*

4. Mostly glabrous; upper petals not backed with brown; stipules more or less scarious, entire ..... 9. *V. glabella*

3. Plants erect, ascending, or prostrate; leaves and flowers scattered along stems; leaves various; capsule pubescent or glabrous, obtuse.

4. Stems prostrate or ascending; leaves orbicular or nearly so, puberulent.

5. Stems long, prostrate, rooting; leaves coriaceous, evergreen, mostly with an apical point. Transition Zone 5. *V. sempervirens* subsp. *typica*

5. Stems weak, ascending; foliage annual or evergreen. Above Transition Zone.

6. Basal leaves evergreen, mostly without apical point; stems short, ascending, 1–2 nodes with undeveloped leaves. Canadian Zone.. 5a. *V. sempervirens* subsp. *orbiculata*

6. Leaves thin, annual, orbicular to reniform; stems of 1–3 nodes with fully developed leaves. Boreal Zone ..... 6. *V. biflora*

4. Stems erect or ascending; at least upper leaves narrowed.

5. Rootstock more or less elongate; flowers 2 cm. or less across; herbage pubescent.

6. Capsules glabrous or glabrate; leaves thin, erect, elongate, elliptic to ovate; pubescence variable but longer than in *V. purpurea*, at least leaf margins ciliate; upper petals usually yellow on back ..... 3. *V. Nuttallii*

6. Capsules appressed puberulent; earliest leaves purplish beneath, orbicular to ovate, irregularly dentate, thicker, less elongate and erect than in *V. Nuttallii;* at least two upper petals brown backed.

7. Later leaves elongate, obtuse, but not linear or canescent (except in subspecies) .... 1. *V. purpurea*

7. Later leaves linear-lanceolate, acute, canescent; flowers smaller than in *V. purpurea;* all petals brown backed ..... 2. *V. pinetorum*
5. Rootstock short and thick, deep seated; flowers more than 2 cm. across; capsules glabrous ..... 4. *V. pedunculata*
2. Corolla white to purple; upper petals reddish violet on back; seeds without caruncle; erect plants; woodlands (except *V. Flettii*).
3. Plants pubescent; leaves rugose.
4. Corolla white with a purple spot near base of lateral petals ..... 14. *V. ocellata*
4. Corolla white on face except for veining.
5. With underground stolons; some leaves wider than long, more pubescent below than above, margins coarsely serrate, ciliate.. 15. *V. rugulosa*
5. Without underground stolons; leaves as long or longer than wide, more pubescent above than below, margins finely serrate, glabrous.
6. Stems 15–35 cm. high; puberulent 16. *V. canadensis*
6. Stems 10–15 cm. high; glabrate.. 17. *V. scopulorum*
3. Plants glabrous; leaf surface not rugose.
4. Corolla white, veined and blotched with purple; leaf blades mainly vertical, cuneate ..... 18. *V. cuneata*
4. Corolla reddish violet, except for yellowish spur; leaves cordate to reniform ... 19. *V. Flettii*

Santa Rosa Junior College,
Santa Rosa, California,
January 15, 1935.

Explanation of the Figures. Plate II

Section Chamaemelanium

Fig. 1. Median vertical section of flower of *Viola Nuttallii* subsp. *praemorsa* × 3.

Fig. 2. Side view and cross section of stamen of *Viola Nuttallii* subsp. *praemorsa* × 10: *a,* anterior appendage; *b,* nectary; *c,* filament; *d,* pollen sac.

Fig. 3. Stamen-sheath and head of style of *Viola sempervirens* subsp. *typica* × 10: *f,* head of style; *e,* stigmatic tube; *g,* bearding of head; *i,* anterior appendages of two ventral stamens; *k,* anther proper; *l,* spur appendages or nectaries; *m,* filament; *n,* receptacle.

Fig. 4. Dorsal view of pistil of *Viola Nuttallii* subsp. *praemorsa* × 10: *a,* head of style; *b,* bearding; *c,* style; *d,* ovary.

Fig. 5. End view of head of style *Viola Nuttallii* subsp. *praemorsa* × 10: *a,* stigmatic tube.

Fig. 6. Side view of *Viola Nuttallii* subsp. *praemorsa* × 10: *a,* stigmatic tube.

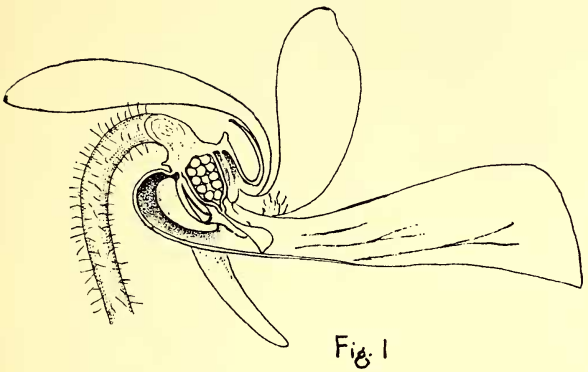
Section Nomimium

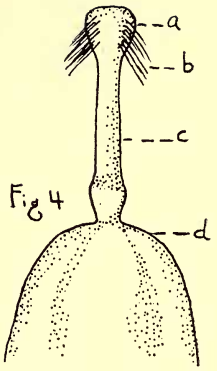
Fig. 7. Median vertical section of flower of *Viola adunca* × 3: *a, d,* anterior appendage of stamen; *b,* head of style; *c,* stigmatic tube; *e,* pollen sac; *f,* ovary; *g,* spur apendage; *h,* bearding of lateral petal.

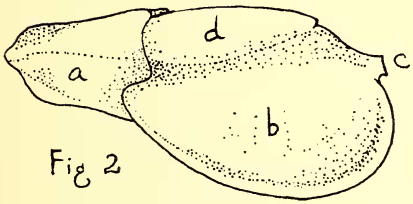
Fig. 8. Side view of ventral stamen of *Viola adunca* × 10: *a,* anterior appendage; *b,* pollen sac; *c,* filament; *d,* spur appendage.

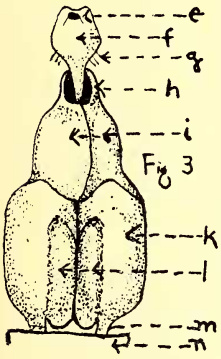
Fig. 9. Side and end views of style of *Viola adunca* × 10: *a,* stigmatic tube; *b,* bearding.

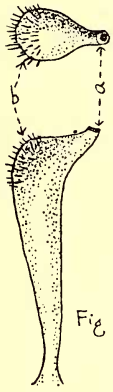
Fig. 10. Dorsal stamen of *Viola adunca* viewed from ovary × 10: *a,* anterior appendage; *b,* pollen sac; *c,* filament.

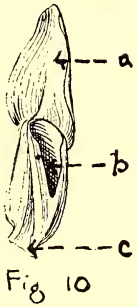


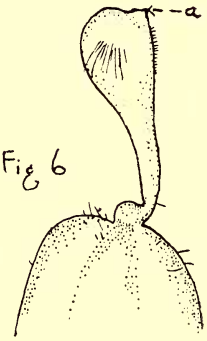


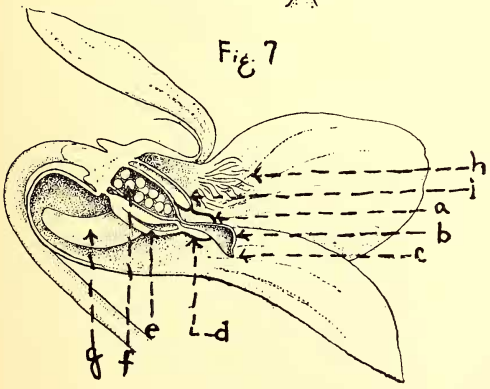












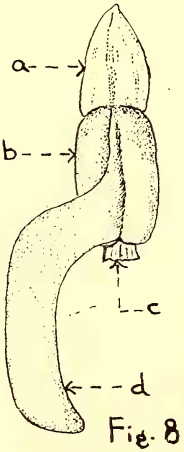


PLATE II. VIOLA: SECTIONS CHAMAEMELANIUM AND NOMIMIUM.